The Brain of *Micropotamogale ruwenzorii* (De Witte and Frechkop, 1955)

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Abstract

Studied the brain of the East-African dwarf otter-shrew, *Micropotamogale ruwenzorii.* It was found to be similar to those of the two other species of otter-shrews, *M. lamottei* and *Potamogale velox*. In nearly all values for relative size of brains and brain parts, *M. ruwenzorii* is intermediate between the other two. *M. lamottei* is closest to the average of Insectivora and *P. velox* is furthest. From the brain characteristics the adaptation for hunting prey in water is lowest in *M. lamottei,* intermediate in *M. ruwenzorii,* and highest in *P. velox*. This is consistent with other physical characteristics. In this sequence, the medulla oblongata and the cerebellum increase, and the olfactory structures decrease. The relative size of the neocortex, which may indicate best the level of brain development, increases from *M. lamottei,* through *M. ruwenzorii,* to *P. velox*. Differences in encephalization indicate that two species of East-African dwarf otter-shrews may exist, but the material at hand is too restricted to substantiate it.

Introduction

In a previous paper (STEPHAN and KUHN 1982) on the brains of African water or otter-shrews (Potamogalinae), several characteristics were described which set the otter-shrew brains apart from most other Insectivora brains investigated. Such characteristics were the tremendous size of the medulla oblongata and the relatively small size of the olfactory structures. The dwarf otter-shrews *(Micropotamogale)* were poorly represented by three imperfectly preserved brains of the West-African form *(M. lamottei).* No brains were available for the East-African form *(M. ruwenzorii),* but brain weights could be determined from the cranial capacities of three skulls. Body weights of *M. ruwenzorii* were taken from RAHM (1960, 1961) and these measures were used to estimate the encephalization of *M. ruwenzorii* in the earlier paper. Since then four new specimens were collected in the stations of the Center of Lwiro of the 'Institut de Recherche Scientifique' (I.R.S.) in the Kivu region of Zaire and their brains were prepared. Our collection of the *Potamogale velox* brains was enlarged by eight specimens.

Based on brain characteristics of *M. ruwenzorii,* this paper focusses on three problems:

1. Are there more than one species of East-African dwarf otter-shrews?
2. Is the brain similar to those of the other Potamogalinae? A positive finding would confirm the general statements on brain evolution and systematic classification made in the previous publication.
3. What is the relative size of structures reflecting the degree of water adaptation?

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Material and methods

The description of the macromorphology is based on four brains (nrs. 3666–3669; Table 1). The median view was graphically reconstructed from the sections of brain 3666. Volumes of the brain parts (Table 2) were determined from the frontally sectioned brains. The brain components and the methods of volume determination as well as volume (and brain weight) comparison were described in detail in previous papers (Stephan and Kuhn 1982; Stephan et al. 1981, 1986), so only brief comments will be given here. Firstly, all volumes were corrected to fresh brain values; secondly, the interspecific comparisons were based on the allometric method. Applying the allometric method, the interdependency of body weight and brain weight or volume of various brain parts was determined by calculating regression lines within groups of closely related species, usually families or subfamilies. When total brain was plotted against body weight, the mean slope of the regression lines was 0.626. This value is the average of the seven slopes of the Insectivora families or subfamilies from which we have at least three species with a relatively large interspecific range of body weights (at least 1:3 from the smallest to the largest species). The slope of the overall Insectivora regression line (with 48 species at hand) is similar (0.642), and was therefore used as the reference baseline in this paper (Fig. 5). Corresponding methods were used for the various brain parts of the 39 species investigated so far; the slopes were between 0.56 and 0.67. The distances of *M. ruwenzorii* or any other species from the reference lines express the degree of deviation from the 'average Insectivora'. They are given in 'allometric indices' and scaled in Figures 6 and 9–11.

Table 1

Data on *Micropotamogale ruwenzorii* collected in the I.R.S. stations in Irangi and Tshibati

animal number	sex	body weight (g)	brain weight (mg)	head + body length (mm)	tail length (mm)	locality	embryos	date of collection
3666	M	117	1237	177	146	Irangi		Feb 2, 1984
3667	F	103	1221	165	140	Irangi	1 small	Feb 3, 1984
3668	F	88	1014	158	142	Tshibati	1 small	Feb 10, 1984
3669	M	86	1063	155	138	Tshibati		Feb 10, 1984

Table 2

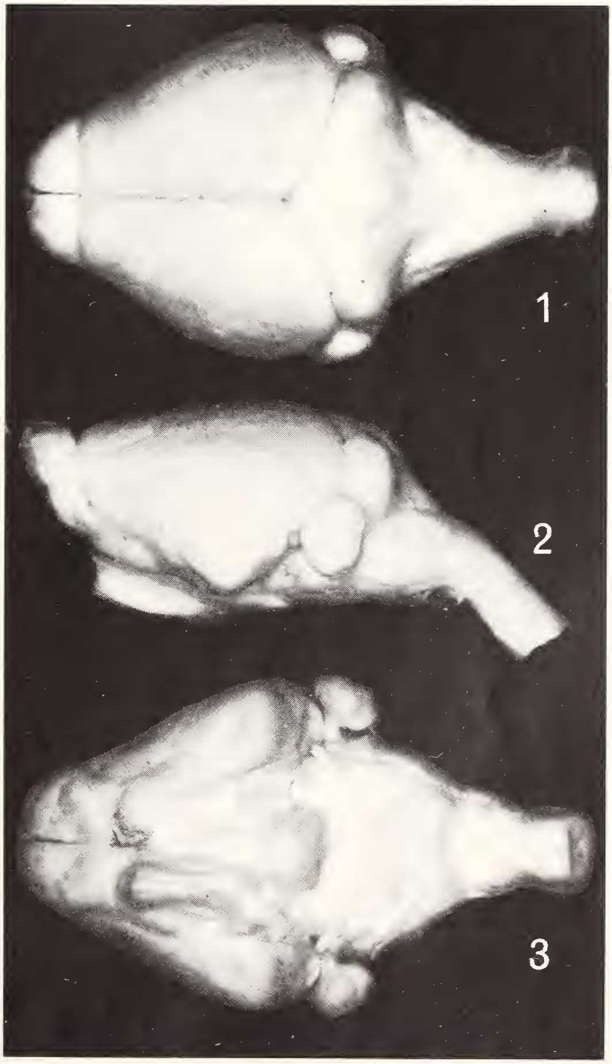
Volumes of brain components
(n = number of individuals)

	Irangi animals				Tshibati animals				Total	
	3666	3667	average (n = 2)	CV	3668	3669	average (n = 2)	CV	average (n = 4)	CV
Ventricle	6.3	6.1	6.2	2.1	10.3	10.0	10.1	2.0	8.2	27.5
Rest	29.0	23.4	26.2	2.0	18.7	20.1	19.4	5.1	22.8	20.1
Net volume	1158.7	1149.0	1153.8	0.6	949.8	996.0	972.9	3.4	1063.3	10.0
Medulla obl.	199.8	208.8	204.3	3.1	179.2	201.2	190.2	8.2	197.2	6.4
Cerebellum	152.5	163.8	158.1	5.0	145.8	133.5	139.6	6.3	148.9	8.5
Mesencephalon	78.7	76.9	77.8	1.6	66.6	67.5	67.0	1.0	72.4	8.7
Diencephalon	101.0	90.3	95.7	7.9	75.4	88.6	82.0	11.3	88.8	11.8
Telencephalon	626.6	609.2	617.9	2.0	482.8	504.2	494.0	3.2	556.0	13.0
Bulbus olf.	35.5	35.2	35.4	0.6	29.2	34.8	32.0	12.4	33.7	8.9
Palaeocortex	94.8	83.1	88.9	9.3	74.5	74.0	74.2	0.5	81.6	11.9
Septum	17.5	17.8	17.6	1.1	16.3	17.0	16.7	3.1	17.1	3.7
Striatum	63.6	63.6	63.6	0.1	54.1	56.1	55.1	2.6	59.4	8.4
Schizocortex	41.1	40.8	41.0	0.5	32.0	35.1	33.5	6.4	37.3	12.0
Hippocampus	112.1	106.2	109.2	3.8	85.2	88.5	86.9	2.6	98.0	13.4
Neocortex	262.0	262.5	262.2	0.1	191.5	199.7	195.6	3.0	228.9	16.9

Results

Macromorphology

The shape and macromorphological details of the brain of *M. ruwenzorii* were similar to those of *M. lamottei*. Compared with the drawings of the brain of *M. lamottei* in Stephan and Kuhn (1982) the *M. ruwenzorii* brain is elongated. Its length is about 80 % of the width in *M. ruwenzorii* (Fig. 1) versus about 70 % in *M. lamottei* and thus more similar to the brain of *P. velox* (about 90 %). The olfactory bulbs of *M. ruwenzorii* were relatively flat (Fig. 2) and projected less beyond the neocortical frontal poles than those of *M. lamottei*. As in the other Potamogalinae, a very big trigeminal nerve as well as a very big medulla oblongata were found (Fig. 3). The corpus callosum was relatively large (medial view, Fig. 4). Judging from the well composed arbor vitae, the cerebellum was well developed.



Figs. 1–3. Brain of *M. ruwenzorii* (nr. 3666): Dorsal view *(Fig. 1)*, left side *(Fig. 2)*, and ventral view *(Fig. 3)*. (Linear enlargement 3.1 ×)

Brain size and encephalization

Brain and body size

The four brain weights (Table 1) had an average of 1134 mg, but there were clear differences between those of the animals from Irangi and those from Tshibati. The brains of the Irangi animals weighed an average of 1229 mg and were thus about 18 % heavier than those of the Tshibati animals (1039 mg). Similar differences were found in the cranial capacities of the skulls from the Museum in Tervuren by Stephan and Kuhn (1982, Table 1), but were not emphasized by those authors. From two of the skulls, a distinctly larger average brain weight (1235 mg) was determined than from the third (1062 mg). The median value was 1149 mg, which is close to the average for the weighed brains (1134 mg).

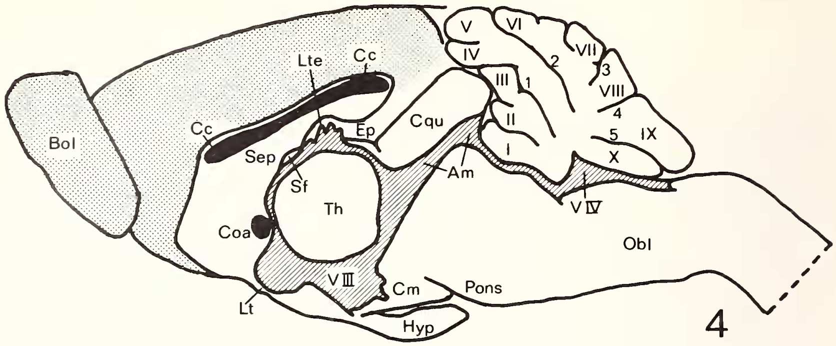


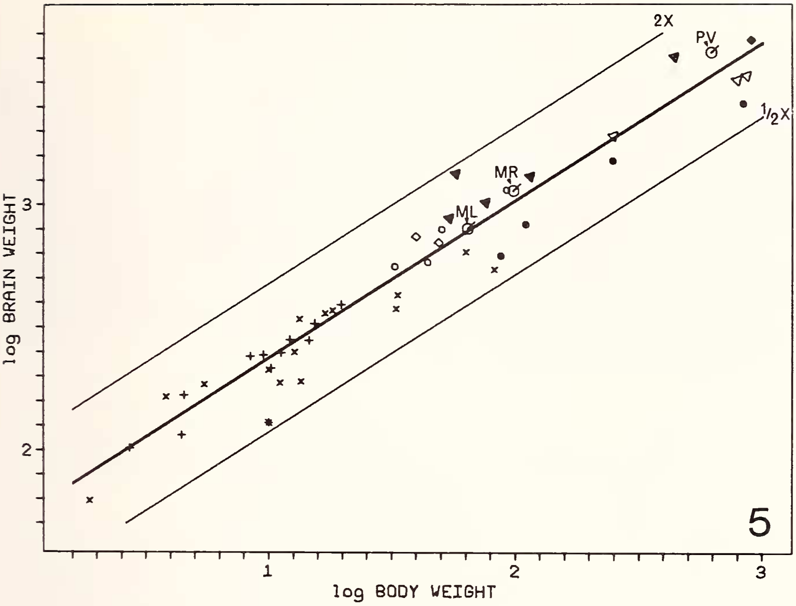
Fig. 4. Mid-sagittal reconstruction of the brain of *M. ruwenzorii.* Linear enlargement 5.0×. Ventricular system is diagonally hatched; surface of cerebral hemispheres adjacent to mid-sagittal plane is marked by dots. Am = aquaeductus mesencephali; Bol = bulbus olfactorius; Cc = corpus callosum; Cm = corpora mamillaria; Coa = commissura anterior; Cqu = corpora quadrigemina; Ep = epiphysis; Hyp = hypophysis; Lt = lamina terminalis; Lte = Lamina tectoria; Obl = medulla oblongata; Sep = septum telencephali; Sf = subfornical body; Th = thalamus; V III = third ventricle; V IV = fourth ventricle. Subdivision of the cerebellar vermis (arbor vitae): 1 = fissura praeculminata; 2 = fiss. prima; 3 = fiss. secunda; 4 = fiss. postpyramidalis; 5 = fiss. posterolateralis; I = lingula; II = lobulus centralis ventralis; III = lobulus centralis dorsalis; IV = lobulus ventralis culminis; V = lobulus dorsalis culminis; VI = declive; VII = tuber vermis; VIII = pyramis; IX = uvula; X = nodulus

This is one more piece of evidence that the cranial capacities provide good approximations to brain weights. The average from the three skulls (1177 mg) is, of course, somewhat higher, since two skulls had large cranial capacities and only one skull had a small capacity. In estimating encephalization, a standard of 1180 mg was applied to *M. ruwenzorii* in the former paper (Stephan and Kuhn 1982). The new standard adopted to take into account possible differences between a smaller and a larger form was 1140 mg, which is intermediary between the average of the four brains (1134 mg) and the median value of the skulls (1149 mg).

The four body weights (Table 1) showed similar differences to the brain weights. Those of the two Irangi animals (110 g) were about 26 % higher than those of the two Tshibati animals (87 g). The overall average was 98.5 g. This again is similar to the value determined in 1982 from four body weights by Rahm (1960, 1961). That average was 95 g, but one of the body weights given was distinctly higher (135 g) than the average of the other three (82 g). As a new standard, a body weight of 98 g was adopted for the present paper.

Encephalization was calculated (1) for the standard brain and body weights, (2) for the average of the four animals caught in Zaire and (3) for the two groups of the Irangi and Tshibati animals separately.

The widening of our collection of *P. velox* by eight animals slightly modified the standard body weight of this species, whereas the standard brain weight remained unchanged. The average body weight of the five animals in the smaller collection was 660 g, and the average brain weight was 4164 mg. The eight new animals had an average body weight of 592 g and an average brain weight of 4145 mg, and thus, the new average for the total collection (n = 13) is 618 g body weight and 4152 mg brain weight, and a new standard of 620 g/4160 mg was introduced. The smaller standard body weight led to a slightly higher index of encephalization compared with that given by Stephan and Kuhn (1982). In addition, the distinct enlargement of the Insectivora reference base (now 48 versus formerly 26 species) and the elimination of the two species of Macroscelididae from the reference base result in slight changes in the slope and the y-intercept of the reference line.



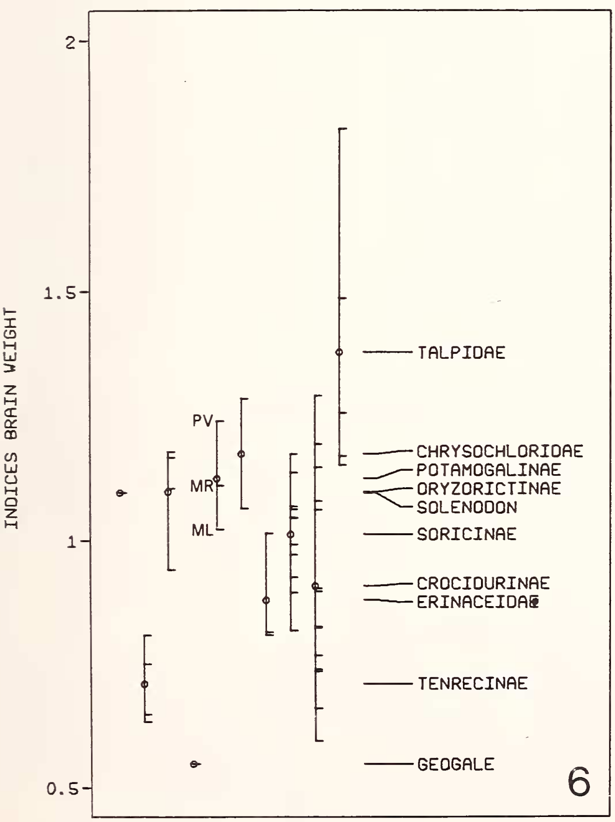


Fig. 5. Brain weight (in milligrams) plotted against body weight (in grams) in a double logarithmic scale. The reference baseline (thick) is the least-square regression line of the 48 species of Insectivora from which brains and body weights were available. The equation is:
log brain weight = 1.733 + 0.642 · log body weight
The thinner parallel lines are in distances of 0.301, i.e. in multiples and fractions of 2; they correspond to the indices scaled in Fig. 6. ML = *M. lamottei;* MR = *M. ruwenzorii;* PV = *P. velox;* ◇ Chrysochloridae; × Crocidurinae; ◁ Erinaceidae; ⁎ *Geogale aurita* (data taken from Rehkämper et al. 1986); ○ Oryzorictinae; ⌀ Potamogalinae; ◆ *Solenodon paradoxus;* + Soricinae; ◀ Talpidae; ● Tenrecinae. – *Fig. 6.* Encephalization indices. The indices are numerical values of the distances from the reference line in Fig. 5. This line represents the average Insectivora and all points on it have an index of 1. Each of the small horizontal bars represents the encephalization index for a species. On the left, the range (vertical bars) and the mean (○) of the various taxonomic units are given, while on the right, the sequence of the means is scaled and the names of the units are given. ML = *M. lamottei;* MR = *M. ruwenzorii;* PV = *P. velox*

Encephalization

The averages were found to be 110 g body weight and 1229 mg brain weight for the larger Irangi animals and 87 g body weight and 1039 mg brain weight for the smaller Tshibati animals. These data result in encephalization indices of 1.11 and 1.09, with an average of 1.10; the index obtained from the standard (98 g/1140 mg) is 1.11. All these values are similar. The corresponding index of *M. lamottei* was 1.02 and that of *P. velox*, 1.24. Thus, within Potamogalinae, the encephalization of *M. ruwenzorii* is intermediary between that of *M. lamottei* (lower) and that of *P. velox* (higher). The mean encephalization of the three species of Potamogalinae (av. 1.12) was slightly above the average of the Insectivora, which is 1. The average indices of the families or subfamilies of Insectivora are scaled in Figure 6. Despite the similar encephalization in Potamogalinae and Oryzorictinae, the composition of the brains may be distinctly different in the two groups.

Table 3

Main brain components expressed as percentages of net brain volume and telencephalic components expressed as percentages of the telencephalon

(n = number of individuals; N = number of species)

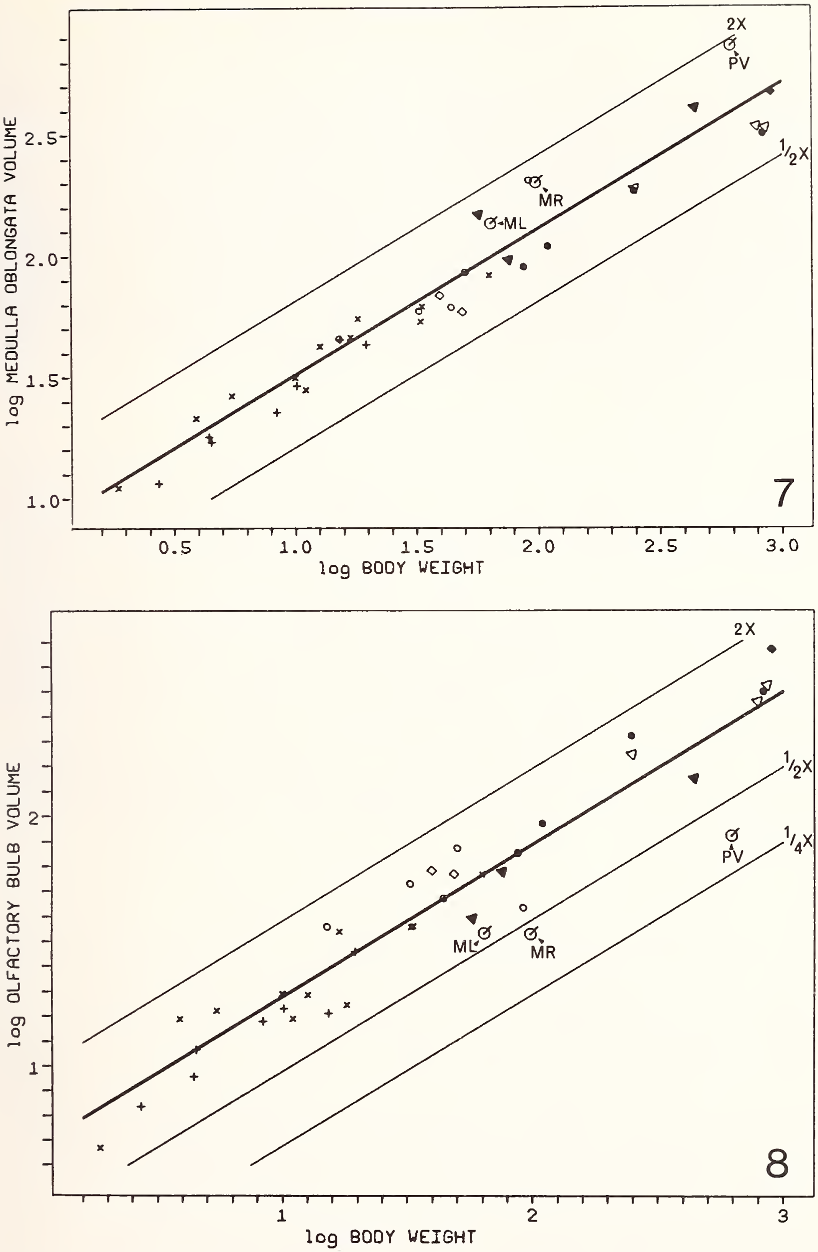
	Irangi animals			Tshibati animals			Species averages			Average	Average
	3666	3667	aver. (n = 2)	3668	3669	aver. (n = 2)	M. ruw. (n = 4)	M. lam. (n = 3)	P. vel. (n = 5)	Potamogalinae (N = 3)	Insectivora (N = 39)
Medulla obl.	17.2	18.2	17.7	18.9	20.2	19.5	18.6	18.2	18.7	18.5	13.7
Cerebellum	13.2	14.2	13.7	15.4	13.4	14.4	14.0	11.1	16.1	13.7	12.8
Mesencephalon	6.8	6.7	6.7	7.0	6.8	6.9	6.8	7.9	6.7	7.1	6.3
Diencephalon	8.7	7.9	8.3	7.9	8.9	8.4	8.4	8.4	7.7	8.2	7.3
Telencephalon	54.1	53.0	53.6	50.8	50.7	50.8	52.2	54.4	50.8	52.5	59.9
Bulbus olfact.	5.7	5.8	5.7	6.0	6.9	6.5	6.1	8.4	4.3	6.3	14.0
Palaeocortex	15.1	13.6	14.4	15.4	14.6	15.0	14.7	16.7	9.7	13.7	25.8
Septum	2.8	2.9	2.9	3.4	3.4	3.4	3.1	3.7	2.5	3.1	2.8
Striatum	10.1	10.5	10.3	11.2	11.1	11.1	10.7	8.1	7.5	8.8	8.7
Schizocortex	6.6	6.7	6.6	6.6	7.0	6.8	6.7	8.2	6.3	7.0	5.7
Hippocampus	17.9	17.4	17.7	17.7	17.5	17.6	17.6	19.2	16.4	17.7	16.0
Neocortex	41.8	43.1	42.5	39.7	39.5	39.6	41.1	35.7	53.3	43.4	27.0

Table 4

Allometric indices of the brain components

(average Insectivora = 1; n = number of individuals; N = number of species)

	Irangi animals			Tshibati animals			Species averages			Average
	3666	3667	aver. (n = 2)	3668	3669	aver. (n = 2)	M. ruw. (n = 4)	M. lam. (n = 3)	P. vel. (n = 5)	Potamogalinae (N = 3)
Medulla obl.	1.41	1.59	1.50	1.50	1.71	1.60	1.55	1.37	1.88	1.60
Cerebellum	1.04	1.22	1.13	1.21	1.13	1.17	1.15	.85	1.40	1.14
Mesencephalon	1.22	1.28	1.25	1.21	1.25	1.23	1.24	1.29	1.51	1.35
Diencephalon	1.25	1.21	1.23	1.11	1.33	1.22	1.23	1.14	1.28	1.22
Telencephalon	.97	1.03	1.00	.89	.95	.92	.96	.91	1.09	.99
Bulbus olfact.	.42	.45	.43	.41	.49	.45	.44	.58	.36	.46
Palaeocortex	.62	.58	.60	.57	.57	.57	.59	.62	.48	.56
Septum	1.00	1.10	1.05	1.11	1.18	1.14	1.10	1.24	1.04	1.13
Striatum	1.14	1.23	1.18	1.15	1.21	1.18	1.18	.84	.98	1.00
Schizocortex	1.08	1.17	1.12	1.01	1.13	1.07	1.10	1.28	1.10	1.16
Hippocampus	1.17	1.19	1.18	1.04	1.10	1.07	1.12	1.13	1.32	1.19
Neocortex	1.40	1.53	1.46	1.23	1.31	1.27	1.37	1.15	1.87	1.46



Figs. 7–8. Volume of brain structures (in mm^3) plotted against body weights (in gram) in double logarithmic scales. *Fig. 7.* medulla oblongata; *Fig. 8.* olfactory bulb. The reference baselines (thick) are the least-square regression lines of the 39 species of Insectivora for which volume measurements were available. Their equations are:

log volume medulla oblongata = 0.910 + 0.60 · log body weight

log volume olfactory bulb = 0.668 + 0.61 · log body weight.

For further explanations and abbreviations, see Fig. 5

Composition of the brain

The average volumes of the various structures of *M. ruwenzorii*, and the coefficients of variation (CV = standard error of the mean in percent of the mean) are given in Table 2. The variation in size was (1) largest in the ventricles and in the rests (meninges, hypophysis, nerves, etc.), and was (2) in general larger in the total material than in the two groups, due to their distinctly different brain sizes. Within the two groups, the greatest variation in size was found in the olfactory bulbs and the diencephalon of the Tshibati animals. The differences seem to be mainly due to true intragroup variation rather than to difficulties in the delineations. Structures difficult to precisely delineate in the serial sections, such as the mesencephalon, may have lower CVs than those easier to delineate (e.g. olfactory bulbs). Similar results were obtained from data of 165 brains of Insectivora and Primates (STEPHAN et al. 1981); furthermore, the CVs (mostly lower than 10) were similar.

Percentages

The main components of the brain expressed as percentages of the net brain volume and of the telencephalic components as percentages of the telencephalon are given in Table 3. The greatest differences between the two groups were in the medulla oblongata, which was smaller in the Irangi animals than in the Tshibati animals, and in the neocortex, which was larger in the Irangi animals. Compared with *M. lamottei* and *P. velox*, the percentages of *M. ruwenzorii* are mostly intermediate and thus the percentages are generally close to the average of the three otter-shrew species. Compared with the average of Insectivora, *M. ruwenzorii* (and thus Potamogalinae in general) have a distinctly higher percentage in neocortex and medulla oblongata and a distinctly lower percentage in olfactory bulb and palaeocortex (cf. Table 3, last columns).

Since the percentages of the various structures are not independent of each other (e.g. the low percentage of the olfactory structures tends to increase the percentages for all other telencephalic parts), allometric indices were used for interspecific comparisons.

Allometric indices

The allometric indices given here indicate the deviation of *M. ruwenzorii* from an 'average Insectivora' of equal body weight. The index of the 'average Insectivora' is, by definition, 1. The greatest positive deviation from 1 was found in the medulla oblongata, and the values indicate that this structure is 1.5–1.6 times larger in *M. ruwenzorii* than in the average Insectivora (Table 4). Next to the medulla oblongata was the neocortex (1.3–1.5 times greater). The greatest negative deviation from 1 was found in the olfactory structures: accessory bulb (< 0.4), main bulb (0.44) and palaeocortex (about 0.6). Thus, the telencephalon as a whole was also relatively small. Compared with the other Potamogalinae, the indices of most structures in *M. ruwenzorii* were intermediate between those of *M. lamottei* and those of *P. velox*. The structures described above as strongly deviating in *M. ruwenzorii* from the average Insectivora all (except striatum) deviated still more in *P. velox* and less in *M. lamottei*. The striatum was relatively small in *P. velox* and *M. lamottei* and relatively large in *M. ruwenzorii*. Since *M. ruwenzorii* is generally intermediate between the two other Potamogalinae, most of its indices were close to the average of Potamogalinae. The greatest differences among the three species were mainly between *M. lamottei* and *P. velox* (Table 4, columns 7–9).

The largest differences between the Irangi and Tshibati animals were in the neocortex, whose indices were about 15 % larger in the Irangi than in the Tshibati animals. Similar but less strong differences existed in the hippocampus (10 %) and in the telencephalon as a whole (9 %). Relatively smaller indices in the Irangi animals were found in the septum (− 8 %) and the medulla oblongata (− 6 %).

Discussion

The brain of *M. ruwenzorii* compared with those of other otter-shrews

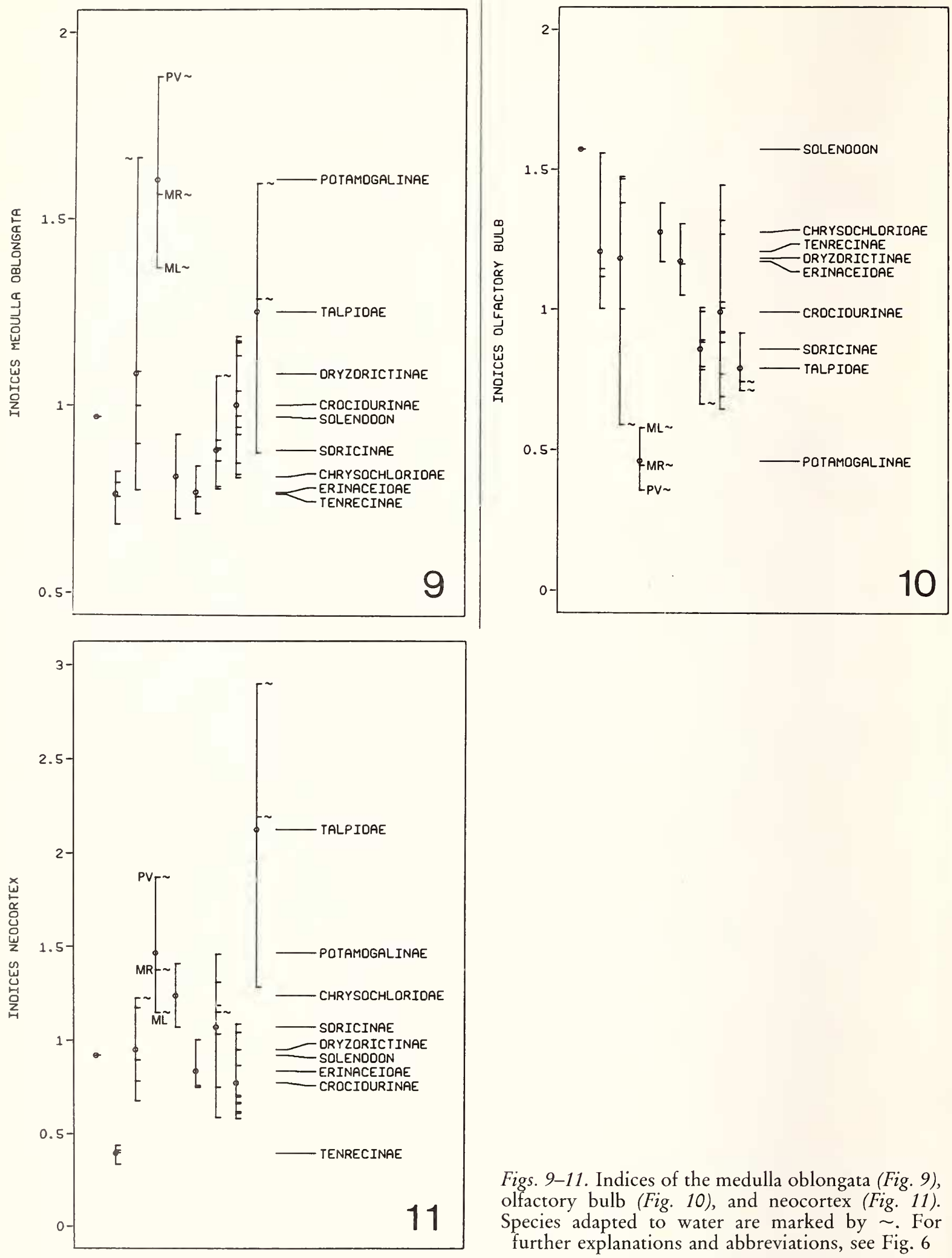
The brain of *M. ruwenzorii* is similar to those of the other two species of otter-shrews; this fully confirms the characteristics generally ascribed to otter-shrew brains. These have been reviewed by Stephan and Kuhn (1982). From the values obtained *M. ruwenzorii* is generally close to the average for the Potamogalinae and ranks between *M. lamottei* and *P. velox*. The accessory olfactory bulb was found to be minute in *M. ruwenzorii*, which is consistent with *M. lamottei*, but in clear contrast to *P. velox*.

Analysis of the differences between Irangi and Tshibati animals

The Irangi animals were larger than the Tshibati animals both in body and brain weights, and our first belief was that these differences may be related to differences in the altitude of the habitats (Irangi 850 m; Tshibati 2200 m). Furthermore, the two skulls with large cranial capacities (see Table 1 in Stephan and Kuhn 1982) were from locations with relatively lower altitudes (642 m and 1090 m) (personal information of Dr. Louette, Museum Tervuren, Belgium), whereas the skull with the smaller cranial capacity was from the region of Butembo, which, according to Rahm (1960), has an altitude of about 1770 m. Therefore, it is possible that a larger 'lowland form' is separable from a smaller 'highland form'. However, there seems to be a discrepancy in the body weights given by Rahm (1960, 1961): the very large body weight of 135 g (Rahm 1961) seems to be from an animal of the Tshibati region. This body weight, however, is from a captive animal and thus may be due to (long-term?) captivity.

This raised the question of whether the differences were sufficient to suggest that two species were distinct or whether they were within the range of intraspecific variation? With regard to encephalization, the slopes of the *intra*specific regression lines were generally between 0.2 and 0.3 whereas *inter*specific ones within genera, subfamilies and families, between 0.5 and 0.7 (Stephan et al. 1986). Regression analyses of the data of *M. ruwenzorii* (Table 1) resulted in a slope of 0.632 when all four individuals were included and reached 0.716 when the two averages (87 g/1039 mg and 110 g/1229 mg) were combined. Both slopes clearly suggest that the groups should be given species rank. Furthermore, generally high variability was found when the two groups (CV values in Table 2, last column) were combined. For many structures, the variability which normally exists within a species, is exceeded. Within the two groups, the variability for most structures was considerably lower (columns 4 and 8).

Another reason for the differences could be that the Tshibati animals were younger than the Irangi animals. However, in mammalian species, juvenile individuals show generally greater encephalization than adults, since the brain grows faster than the body in early development. The brain generally arrives at (or even exceeds) its final size in juveniles, whereas the body increases more slowly over a much longer period. In the smaller and thus possibly younger Tshibati animals no such juvenile excess in encephalization was found. The encephalization indices were, on the contrary, even slightly lower (1.09 versus 1.11). However, it may well be that strongly water adapted mammalian species (such as otters, seals, and whales) deviate from the general rule of early finished brain growth and may have not only a long period of body growth but also long brain growth. In such cases, the brain/body weight relation would not necessarily follow the intraspecific slope, but could rather produce a higher one. In *P. velox*, the possibility of such a deviation from the norm



Figs. 9–11. Indices of the medulla oblongata *(Fig. 9)*, olfactory bulb *(Fig. 10)*, and neocortex *(Fig. 11)*. Species adapted to water are marked by ~. For further explanations and abbreviations, see Fig. 6

can be deduced from the data given by STEPHAN and KUHN (1982, Table 1). In the five specimens, the heavier individuals had the larger brains; the regression line for the five animals had a slope of 0.595, which otherwise is typical for interspecific comparisons. However, when the new data were included (now from 13 individuals) the slope decreased to 0.340, which is close to the values generally found within species. The question of whether otter-shrews show long-lasting body and brain growths must remain open and, as must finally, the question of whether the Irangi and Tshibati animals belong to two different species. The material at hand is not sufficient for a final decision.

Water adaptation

The quantitative characteristics of otter-shrew brains are similar to those found in other species with similar water adaptations, such as *Limnogale* (Oryzorictinae), *Neomys* (Soricinae), *Galemys* and *Desmana* (Talpidae). They were summarized by STEPHAN and KUHN (1982). The most striking brain characteristics of water-adapted Insectivora (marked by ~ in Figs. 9 and 10) are the large medulla oblongata (Fig. 9) and the small olfactory bulb (Fig. 10). The relative size of the cerebellum may also be indicative. If these characteristics are taken as an index of water adaptation, *M. lamottei* is the least adapted, and *P. velox*, the most adapted. For *M. ruwenzorii*, an intermediate degree of water adaptation is indicated. This is in agreement with the findings of HEIM DE BALSAC (1954, 1956, 1957), HEIM DE BALSAC and BOURLIERE (1955), DE WITTE and FRECHKOP (1955), GUTH et al. (1959, 1960), RAHM (1961), and DUBOST (1965), which suggest that *M. ruwenzorii* is better adapted to catch prey in water than *M. lamottei*, but less than *P. velox*. In contrast to *M. lamottei*, *M. ruwenzorii* has webbed hands and feet, but in contrast to *P. velox*, no laterally compressed tail.

Brain evolution and classification of otter-shrews

With regard to both the brain evolution and the classification of otter-shrews, the findings on *M. ruwenzorii* confirm the statements of STEPHAN and KUHN (1982). Quantitative investigations in a series of primates, which order includes the most highly evolved mammalian species in terms of brain development, have shown that the neocortex is by far the most progressive structure. With regard to their neocorticalization, Potamogalinae are in the upper half of the total range found in Insectivora (Fig. 11), with *M. ruwenzorii* close to the average of otter-shrews and *M. lamottei*, distinctly lower, close to the average of all Insectivora. This is in accordance with the anatomical and behavioural investigations of HEIM DE BALSAC (1954, 1956), GUTH et al. (1960), VERHEYEN (1961 a, b) and DUBOST (1965), indicating that *M. lamottei* is closer to the basic forms than *M. ruwenzorii* and *P. velox*.

With reference to brain characteristics, the otter-shrews may best be classified as a subfamily (Potamogalinae) of the Tenrecidae. The dwarf otter-shrews, especially *M. lamottei*, may mediate between Oryzorictinae and *P. velox* (for more details see STEPHAN and KUHN 1982).

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Zusammenfassung

Das Gehirn von Micropotamogale ruwenzorii (De Witte and Frechkop, 1955)

Das Gehirn der ostafrikanischen Kleinotterspitzmaus, *M. ruwenzorii*, zeigt gute Übereinstimmung mit den Gehirnen der westafrikanischen Kleinotterspitzmaus, *M. lamottei*, und der Großotterspitzmaus, *P. velox*. Fast alle Indices der relativen Größe des Gehirns und der Hirnteile liegen bei *M. ruwenzorii* zwischen jenen der beiden anderen Arten. *M. lamottei* liegt dem Durchschnitt der Insectivora am nächsten, *P. velox* am fernsten. In Einklang mit anderen Merkmalen weisen die Hirncharakteristika darauf hin, daß die Anpassung an die Nahrungsjagd im Wasser bei *M. lamottei* am geringsten, bei *M. ruwenzorii* stärker und bei *P. velox* am stärksten ist. In dieser Reihenfolge nehmen die Medulla oblongata und das Kleinhirn relativ zu, während die olfaktorischen Strukturen abnehmen. Die relative Größe des Neocortex, die das Evolutionsniveau des Gehirns einer Art am besten anzeigt, nimmt ebenfalls von *M. lamottei* über *M. ruwenzorii* zu *P. velox* zu. Unterschiede in der Encephalisation lassen es möglich erscheinen, daß zwei Arten von ostafrikanischen Kleinotterspitzmäusen existieren. Das verfügbare Material ist für eine endgültige Stellungnahme jedoch zu gering.

References

De Witte, G.-F.; Frechkop, S. (1955): Sur une espèce encore inconnue de mammifère africain, *Potamogale ruwenzorii*, sp. n. Bull. Inst. roy. Sci. Nat. Belgique **31**, Nr 84, 1–11.

Dubost, G. (1965): Quelques renseignements biologiques sur *Potamogale velox*. Biol. gabon. **1**, 257–272.

Guth, Ch.; Heim de Balsac, H.; Lamotte, M. (1959): Recherches sur la morphologie de *Micropotamogale lamottei* et l'évolution des Potamogalinae. I. Ecologie, denture, anatomie crânienne. Mammalia **23**, 423–447.

— — — (1960): Recherches sur la morphologie de *Micropotamogale lamottei* et l'évolution des Potamogalinae. II. Rachis, viscères, position systématique. Mammalia **24**, 190–217.

Heim de Balsac, H. (1954): Un genre inédit et inattendu de Mammifère (Insectivore Tenrecidae) d'Afrique Occidentale. Comptes rendus des séances de l'Académie des Sciences **239**, 102–104.

— (1956): Morphologie divergente des Potamogalinae (Mammifères Insectivores) en milieu aquatique. Comptes rendus des séances de l'Académie des Sciences **242**, 2257–2258.

— (1957): Évolution des vertèbres caudales chez les Potamogalinae (Mammifères Insectivores Tenrecidae). Comptes rendus des séances de l'Académie des Sciences **245**, 562–564.

Heim de Balsac, H.; Bourlière, F. (1955): Ordre des Insectivores, Systématique. In: Traité de Zoologie. Ed. by Grassé, P.-P. Paris: Masson. Vol. **17**, 1653–1697.

Rahm, U. (1960): Note sur les spécimens actuellement connus de *Micropotamogale (Mesopotamogale) ruwenzorii* et leur répartition. Mammalia **24**, 511–515.

— (1961): Beobachtungen an der ersten in Gefangenschaft gehaltenen *Mesopotamogale ruwenzorii* (Mammalia-Insectivora). Rev. Suisse Zool. **68**, 73–90.

Rehkämper, G.; Stephan, H.; Poduschka, W. (1986): The brain of *Geogale aurita*, Milne-Edwards and Grandidier, 1872 (Tenrecidae, Insectivora). J. Hirnforsch. (in print).

Stephan, H. (1972): Evolution of primate brains: A comparative anatomical investigation. In: The Functional and Evolutionary Biology of Primates. Ed. by Tuttle, R., 155–174. Chicago: Aldine/Atherton Inc.

Stephan, H.; Baron, G.; Frahm, H. D. (1986): Comparative size of brains and brain components. In: Comparative Primate Biology. Vol. **III**; Neurosciences. Ed. by Steklis, H. New York: Liss Inc. (in print).

Stephan, H.; Frahm, H.; Baron, G. (1981): New and revised data on volumes of brain structures in insectivores and primates. Folia primatol. **35**, 1–19.

Stephan, H.; Kuhn, H. J. (1982): The brain of *Micropotamogale lamottei* Heim de Balsac, 1954. Z. Säugetierkunde **47**, 129–142.

Verheyen, W. N. (1961a): Recherches anatomiques sur *Micropotamogale ruwenzorii*. 1. La morphologie externe, les viscères et l'organe génital mâle. 2. La myologie de la tête, du cou et de la patte antérieure. Bull. Soc. Roy. Zool. Anvers **21**.

— (1961b): Recherches anatomiques sur *Micropotamogale ruwenzorii*. 3. La myologie de la patte postérieure, de la région sacrale et de la queue. 4. Observations ostéologiques et considérations générales. Bull. Soc. Roy. Zool. Anvers **22**.

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